Movement Ecology of the Reef Manta Ray

*Manta alfredi* in the Eastern Red Sea

Thesis by:

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ABSTRACT

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Many well-studied elasmobranch populations have recently exhibited significant decline. The limited data related to fisheries and sightings for many unstudied or poorly understood populations indicate that these are also suffering. Directed fisheries and more cryptic threats such as entanglement and vessel strike represent significant risk to mobulid rays, arguably one of the most vulnerable elasmobranch groups. Very little information currently exists describing the basic ecology of manta rays or quantifying anthropogenic threats and impacts; however, recent efforts have drastically improved the body of knowledge available for these species, including oceanographic influences on movement, seasonal migration, and mating behaviors. Nevertheless, Red Sea mantas remain completely enigmatic. In this thesis, Chapter 1 details results from tagging 18 reef manta rays *Manta alfredi* in the eastern Red Sea using satellite and acoustic tag technology and demonstrates that mantas occupy areas with high human traffic. The combined satellite and acoustic techniques define both regional movements and ‘hotspots’ of habitat use where there is significant potential for manta-human interaction. I also present opportunistic sighting data that corroborate anthropogenic impacts on this population. Chapter 2 explores the vertical component of the nine satellite tags that were deployed on *Manta alfredi* as described in the previous chapter. Seven tags returned adequate data for analysis. Three of the seven were physically recovered yielding full archival datasets of depth, temperature, and light levels every 10-15 seconds for over 2.6
million cumulative data points. Mantas frequented the upper 10 m during the day and occupied deeper water through nocturnal periods. Individuals also exhibited deep diving behavior as deep as 432 m, extending the known depth range of the species. An investigation of 76 high-resolution deep dives suggests gliding is a significant behavioral component of these dives and may provide an efficient mechanism for travel compared to continuous horizontal swimming. This study is the first to employ satellite telemetry techniques on *Manta alfredi* and is the only study directed at mobulids in the Red Sea. A holistic understanding of these behaviors is essential for developing and implementing appropriate management techniques, and this work is particularly timely in light of recent international trade regulation as mantas were listed on Appendix II of the Convention on International Trade in Endangered Species.
ACKNOWLEDGEMENTS

I would like to thank Jesse Cochran for his help with the entire acoustic component of this project from monitor deployment and maintenance to data acquisition. He also contributed very valuable discussion over the course of many late nights in the field. Many thanks to all those who provided field support for this work including Mark Priest, Tane Sinclair-Taylor, Lizzie Tyler, Fernando Cagua, Pedro De La Torre, Maha Khalil, Jessica Bouwmeester, Julia Spät, Gerrit Nanninga, Dream Divers, and many others. I also express a sincere thank you to Ben Galuardi for his tireless assistance with all questions of satellite tag analysis. Co-authors on the resulting manuscripts will include Gregory B. Skomal (Massachusetts Fisheries), Michael L. Berumen (KAUST), and Simon R. Thorrold (WHOI). This project was supported by several funding sources, including the Red Sea Research Center, KAUST awards nos. USA 00002 and KSA 00011 to SRT, as well as KAUST baseline funding and competitive awards to MLB.
TABLE OF CONTENTS

Committee Approval Form ............................................................................................................... 2
Copyright ........................................................................................................................................ 3
Abstract ......................................................................................................................................... 4
Acknowledgements ....................................................................................................................... 6
Table of Contents .......................................................................................................................... 7
List of Abbreviations ..................................................................................................................... 8
List of Figures ............................................................................................................................... 9
List of Tables ................................................................................................................................... 10
General Introduction ...................................................................................................................... 11
Chapter 1: Telemetry techniques bridge the gap to Manta conservation
  1.1 Abstract .................................................................................................................................... 14
  1.2 Introduction ........................................................................................................................... 15
  1.3 Methods
    1.3.1 Study Area .................................................................................................................... 18
    1.3.2 Satellite Telemetry ........................................................................................................ 20
    1.3.3 Acoustic Telemetry ...................................................................................................... 23
  1.4 Results ..................................................................................................................................... 23
  1.5 Discussion ............................................................................................................................. 26
Chapter 2: Diving behavior of the reef manta ray (Manta alfredi)
  2.1 Abstract .................................................................................................................................... 33
  2.2 Introduction ........................................................................................................................... 34
  2.3 Methods .................................................................................................................................. 35
  2.4 Results ..................................................................................................................................... 37
  2.5 Discussion ............................................................................................................................. 42
Conclusion ......................................................................................................................................... 49
Supplemental Figure ..................................................................................................................... 50
References ......................................................................................................................................... 51
LIST OF ABBREVIATIONS

**CITES**: Convention on International Trade in Endangered Species of Wild Fauna and Flora

**CMS**: Convention on the Conservation of Migratory Species of Wild Animals

**DVM**: diel vertical migration

**FAO**: Food and Agriculture Organization of the United Nations

**GBR**: Great Barrier Reef, Australia

**GPS**: Global Positioning System

**IUCN**: International Union for the Conservation of Nature

**K-S**: Kolmogorov-Smirnov statistical test

**KSA**: Kingdom of Saudi Arabia

**MK10-AF**: MK10 satellite tag with Fastloc GPS technology

**mP**: MiniPat satellite tag technology

**MPA**: marine protected area

**PSAT**: Pop-up Satellite Archival Transmitting

**SD**: standard deviation
LIST OF FIGURES

Figure 1.1. Most probable tracks for five satellite tagged reef manta rays
*Manta alfredi* in the Red Sea. ................................................................. 18
Figure 1.2. Acoustic receivers deployed in the Al Lith region and acoustic
detections made ................................................................................. 22
Figure 1.3. Tracks for *Manta alfredi* tagged with global positioning system
(GPS) tags ............................................................................................ 24
Figure 1.4. Composite time-at-depth histogram for seven reef manta rays
with satellite tags .................................................................................. 25
Figure 1.5. Acoustic detections of individual *Manta alfredi* on all receivers.... 26
Figure 1.6. Propeller strike and line scars on reef manta rays ....................... 30
Figure 2.1. Site map and *Manta alfredi* tagging locations ............................ 36
Figure 2.2. Daily ambient water temperature and depth experienced by
*Manta alfredi* ....................................................................................... 39
Figure 2.3. Daily depth utilization for *Manta alfredi* ................................. 40
Figure 2.4. Diel percent time-at-depth distribution ..................................... 41
Figure 2.5. Average vertical velocity for three reef manta rays ..................... 42
Figure 2.6. Deep dive velocity histogram .................................................. 44
Figure 2.7. Consecutive deep diving behavior by an individual *Manta
alfredi* and corresponding vertical velocity histogram .......................... 46
Figure S1. Lunar regression with mean daily nighttime depth ....................... 50
LIST OF TABLES

Table 1.1. Satellite tagging summary for nine reef manta rays from the Saudi Arabian Red Sea .......................................................... 19
Table 1.2. Acoustic tagging summary for nine reef manta rays from the Saudi Arabian Red Sea .......................................................... 21
Table 2.1. Statistical results for vertical habitat use and diving behaviors of 7 PSAT tagged *Manta alfredi* .......................................................... 41
GENERAL INTRODUCTION

The genus *Manta* (family *Mobulidae*) contains two species of zooplanktivorous elasmobranchs that are distributed globally in tropical and sub-tropical waters (Couturier et al. 2012). Taxonomic ambiguity has plagued proper classification and, consequently, has hindered appropriate investigation of this group. Historically, the genus was considered monotypic. However, recent morphological (Marshall et al. 2009) and genetic (Kashiwagi et al. 2012) evidence has divided the genus into two species: the giant manta ray *Manta birostris* (Walbaum 1792) and the reef manta ray *Manta alfredi* (Krefft 1868). A third putative species (*M. sp. cf. birostris*) in the Atlantic may be distinct from *M. birostris*, but further investigation is needed to confirm adequate divergence (Marshall et al. 2009). Field identification is difficult and problems are further compounded by varying prevalence of allopatric, parapatric, and sympatric occurrence of the two species across much of their range (Kashiwagi et al. 2011). Thus, interpretation of existing literature (especially pre-2009) must be done with caution [i.e. see Dewar et al. (2008)].

The giant manta ray, *Manta birostris*, is the larger *Manta* spp. (max disc width (*D*<sub>W</sub>): 9.1 m) (Compagno and Last 1999) and is found inhabiting seamounts and offshore islands more frequently than coastal areas (Marshall et al. 2009). Movements into peripheral environments such as the eastern U.S. (Bigelow and Schroeder 1953), southern Brazil (Luiz et al. 2009), and northern New Zealand (Duffy and Abbott 2003), along with preliminary satellite tag studies suggest extensive movements (>1000km) throughout pelagic environments (Rubin et al. 2008). *Manta alfredi* is the smaller, coastal species and exhibits typical K-selected life history traits including slow maturation rate, low reproductive output, and long lifespan. Sighting records suggest preferential occupation
of nearshore waters of the tropics with strong site affinity and limited movements (Marshall et al. 2009) although excursions >500 km have been documented (Couturier et al. 2011). Movements of both species coincide with predictable aggregations at several known locations in tropical and subtropical waters (Couturier et al. 2012) associated with mating, cleaning, food availability, and currents (Dewar et al. 2008; Luiz et al. 2009; Anderson et al. 2011a; Couturier et al. 2011; Jaine et al. 2012).

Saudi Arabia has seen rapid population growth and recent development over the last two decades. In this time, the country’s population has nearly doubled (Central Intelligence CIA 2013), and registered artisanal and industrial fishing boats increased 118 and 148%, respectively, between 1989-2001, further facilitating an industry already operating above capacity (Morgan 2006). This expansion has, at least partially, driven a changing fisheries climate from a community once dominated by artisanal fishers to an increasing number of investor-driven, industrial fishing practices encouraging maximum take and short-term profit (Gladstone 2002). Gladstone (2002) has shown that these evolving fisheries heavily target nursery areas and concentrate efforts within proposed marine protected areas (MPAs). Poor reporting and landings in nearby countries makes quantifying and assessing current stocks difficult. However, using available data, landings appear to have remained relatively steady in the Saudi Arabian Red Sea (~40,000 tonnes/year) since the mid-80s despite a rapidly growing secondary fleet of non-artisanal fishers (Morgan 2006). A few country-specific studies mention elasmobranchs as a component of directed harvest (Gladstone 2002; Morgan 2006; Tsehaye et al. 2007), but no publications address the magnitude of these fisheries in the Red Sea. Unfortunately, FAO reports don’t distinguish among basins when countries
border multiple water bodies (i.e. Arabian vs. Red Sea), and regional fisheries statistics are unreliable measures of actual elasmobranch harvest (Spaet et al. 2012). Finally, Saudi Arabia shares a southern border with Yemen, recently evaluated as a top 20 elasmobranch harvesting country, where reported elasmobranch catches exceeded 12,000 tonnes in 2007 (Lack and Sant 2009). However, despite these reports, it is unlikely that significant fishing pressure is currently exerted on mantas in the Saudi Arabian Red Sea. Fishermen interviews and extensive fish market surveys suggest no directed manta fishery currently exists (J. Spaet, pers. comm.). However, these methods thus far only incorporate domestic fisheries and don’t account for the potentially significant impacts of foreign-based fishermen, international landings, and manta bycatch. Although data is lacking, manta susceptibility to decline is high, and populations are likely to suffer should human-induced manta mortality grow.
Chapter 1: Telemetry Techniques Bridge the Gap to *Manta* Conservation

1.1 ABSTRACT

Global elasmobranch populations are suffering, and mobulid rays have shown particular susceptibility to increased anthropogenic pressures. Directed mobulid fisheries are common in some areas and, combined with more cryptic human-induced threats, may be causing significant declines. Very little information exists describing the basic ecology of manta rays, and none is available for the Red Sea. In this study, eighteen manta rays were fitted with satellite (n=9) and acoustic (n=9) tags in the eastern Red Sea. An extensive acoustic monitoring array (70 receivers) was also deployed to record movements of acoustically tagged fish in the region. Estimated and realized satellite tag tracks indicated regional movements < 200 km from tagging location and a largely coastal orientation. Acoustic results show no seasonality or diel differences in manta occupation of the area but lend strong support for coastal habitation observed in satellite tracks. ‘Hotspots’ of activity were defined with acoustic telemetry and indicate the high likelihood of overlap with areas that exhibit constant human use, creating the potential for strong manta-human interaction. Opportunistic sighting data confirm the occurrence of vessel strike and entanglement in this population that is further substantiated by detailed horizontal and vertical movement data. An understanding of animal behavior is crucial for the appropriate design and implementation of management and conservation techniques. A unique, multifaceted approach employed in this study capitalizes on the strengths of each telemetry technique to yield a more accurate and holistic representation of manta ecology. These results are particularly timely in light of the recent international trade regulation adopted by CITES, established listing on Appendices I and II of Convention
on Migratory Species, and the standing ‘vulnerable to extinction’ assessment by the IUCN.

1.2 INTRODUCTION

In recent years, global elasmobranch populations have experienced serious declines (Dulvy et al. 2008; Ferretti et al. 2010). An estimated 17% of shark species are listed as critically endangered, endangered, or vulnerable to extinction (IUCN 2012) without accounting for gross underreporting of catches (Clarke et al. 2006). There are eleven recognized species of devil rays (Family: Mobulidae) representing two genera: Mobula and Manta. Within this group, one species (9%) of devil ray is listed as endangered and three (27%) as vulnerable to extinction, including both recognized Manta species. Global elasmobranch declines are largely attributed to the rise in demand and value of shark fins, mobulid gill rakers, and other body parts in Asian markets (Shen et al. 2001; Schindler et al. 2002). Mantas, specifically, are valuable for their gill rakers for use in traditional Chinese medicines, and their cartilage is often used in shark fin soup (Shen et al. 2001; Alava et al. 2002). These products drive direct manta ray fisheries and fuel indirect (largely bycatch-driven) harvest throughout much of their range (Alava et al. 2002; Dewar 2002; White et al. 2006). Further and more cryptic threats to mantas include mooring and fishing line entanglement (Bigelow and Schroeder 1953), boat strikes (Deakos 2010) and pressure from ecotourism operations (Dewar et al. 2008; Couturier et al. 2012).

Over the past two decades, harvest bans have been implemented for mantas after some regions began recognizing the fragility of manta populations and, in some cases,
experienced significant regional declines, including the Philippines (Alava et al. 2002),
Indonesia (Dewar 2002; Barnes 2005; White et al. 2006), Japan (Homma et al. 1999),
Mexico (Notarbartolo-di-sciara 1988), and India/Sri Lanka (Anderson et al. 2011b).
Harvest restrictions are now imposed in Hawaii (USA) and the Philippines and within
marine protected areas (MPAs) of Yap and Western Australia. In 1995, the Republic of
the Maldives banned export of rays and their products, effectively curtailing the
development of any commercial fisheries in the country’s waters (Marshall et al. 2011a).
Recently, the Convention on International Trade in Endangered Species (CITES) made a
critical move toward improved manta conservation and management by listing both
manta species on Appendix II. This latest policy measure does not implement any harvest
bans or affect domestic sale of manta products. However, Appendix II does require
documentation for international trade, theoretically enabling much improved
quantification of manta harvest for this lucrative industry. Catches and trade may be
slowly becoming more transparent and readily quantified; yet, many anthropogenic
threats to mantas remain completely enigmatic.

Batoids are demonstrably among the most vulnerable marine fauna to
anthropogenic threats (Dulvy et al. 2008), and mantas are considered particularly
susceptible. Although little information is available, manta rays (like many
elasmobranchs) likely exhibit typical K-selected life history traits including slow
maturation rate, low reproductive output, and long lifespans making them highly
sensitive to exploitation and subsequent decline (Couturier et al. 2012). In addition, small
resident population sizes and production of few offspring likely result in even greater
susceptibility to harvest than many other elasmobranchs (Dewar et al. 2008; Ferretti et al. 2010; Marshall et al. 2011b; Deakos 2012).

The lack of information about key life history traits, population size, movements, and habitat use of mantas is concerning as anthropogenic pressures continue to rise (White et al. 2006). Ecological studies provide crucial insight into the behavior of exploited species that is necessary for developing effective management and conservation strategies. Historically, scientific understanding of the ecology of large pelagic animals was limited to scarce observations, capturing only a tiny percentage, if any, of a species’ behavior. The past decade has brought rapid advances in electronic tagging equipment, which can now provide more detailed information about the movement and habitat use of marine species (Kohler and Turner 2001). Thus far, no published studies have used satellite telemetry techniques to quantify long-term M. alfredi movements and potential interaction with fishing fleets, nor is any ecological or behavioral information available about mantas of the Red Sea. The ecology of Red Sea organisms is generally understudied (Berumen et al. 2013), and the region specifically suffers from a shortage of elasmobranch studies (Spaet et al. 2012). Given this lack of information and the recent international trade regulation adopted by CITES, a detailed investigation of movement and habitat use of this poorly understood and vulnerable marine species is more critical now than ever. The overall aim of this chapter is to present detailed movement data and assess the potential for anthropogenic threats to Manta alfredi in this region as a result of its behavior. If individuals spend more time offshore than inshore, they are less likely to encounter fishing gear and fishing boats. In this chapter, I will examine this component of M. alfredi movement ecology using modern telemetry techniques.
1.3 METHODS

1.3.1 Study Area

The Farasan Banks system occupies over 500 km of coastline in the southeastern Red Sea (Fig. 1.1) and forms a massive island group up to 100 km wide (Antonius et al. 1990). This is a highly productive region that houses a diverse reef community and supports a large portion of Saudi Arabia’s fisheries (Gladstone 2000). Al Lith is a coastal city of Saudi Arabia situated on the northern Farasan Banks that hosts a growing fleet of investor-driven, industrial fishing vessels seeking maximum take and short-term profit and exhibits intensive onshore aquaculture (Gladstone 2002; Jin et al. 2012).

Figure 1.1. Most probable tracks for five satellite tagged reef manta rays *Manta alfredi* in the Red Sea. Estimated movements ranged from the upper Farasan Bank north nearly to Jeddah.
<table>
<thead>
<tr>
<th>Manta ID</th>
<th>Tag Number</th>
<th>Disc Width (cm)</th>
<th>Tag Type</th>
<th>Tag Date</th>
<th>Tag Latitude (°N)</th>
<th>Tag Longitude (°E)</th>
<th>Deployment Duration (days)</th>
<th>Popup Latitude (°N)</th>
<th>Popup Longitude (°E)</th>
<th>Track Distance (km)</th>
</tr>
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<tr>
<td>MA102</td>
<td>95995</td>
<td></td>
<td>MiniPAT</td>
<td>2-Apr-11</td>
<td>20.129</td>
<td>40.217</td>
<td>188</td>
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<td>MiniPAT</td>
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<td>MiniPAT</td>
<td>17-Apr-11</td>
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<td>40.217</td>
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<td></td>
<td>MiniPAT</td>
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<td>20.129</td>
<td>40.217</td>
<td>155</td>
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<td>106759*</td>
<td></td>
<td>MK10-AF</td>
<td>21-Apr-11</td>
<td>20.154</td>
<td>40.229</td>
<td>102</td>
<td>20.158</td>
<td>40.158</td>
<td>15</td>
</tr>
<tr>
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<td>MK10-AF</td>
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<td>40.237</td>
<td>102</td>
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<td>180</td>
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<td>40.2310</td>
<td>DNR</td>
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Table 1.1. Satellite tagging summary for nine reef manta rays (*Manta alfredi*) from the Saudi Arabian Red Sea. Track distance refers to straight-line distance from tagging to popup location. Two satellite tags did not report (DNR). * indicates tag was physically recovered.
1.3.2. Satellite Telemetry

Nine *Manta alfredi* were tagged with pop-up satellite archival tags (PSAT) during the northern hemisphere spring 2011 and 2012 (5 miniPAT, 4 MK10-AF; Wildlife Computers Inc., Redmond, WA, USA) (Table 1.1). Tags were attached to a stainless steel dart with small diameter cable and applied by a freediver into the dorsal musculature near the midline with a sling spear.

PSAT tags recorded light level, depth, and water temperature every 5 and 10 seconds for the miniPAT and MK10, respectively. Data was summarized internally for every 24-hour period into 14 (mP) or 16 (MK10) temperature and depth bins. In addition, depth-temperature profiles were compiled over a 24- (mP) or 12- (MK10) hour period, and light levels were concurrently recorded with depth to incorporate attenuation in post-processing. Both tag types also recorded depth data at higher temporal resolution to enable the reconstruction of dive profiles. The temporal resolution of this data varied between the two tag types (mP: 450sec intervals, MK10: 75sec intervals). The duration of these recordings was either constant (i.e., always on) (mP) or cycled one week on with two weeks off (MK10) for the duration of tag deployment. Automatic pop-up was programmed to initiate after 100 days (MK10) or 180 days (mP). Once released from the ray, the tags transmitted summarized data via the Argos satellite system until battery failure. Initial position estimates were performed using proprietary software provided by the tag manufacturer (WC-GPE; Wildlife Computers) that utilizes threshold light-level geolocation methods (Hill and Braun 2001). Further track optimization was conducted with a state-space unscented Kalman filter model and blended sea surface temperature in the UKFSST library (Lam et al. 2008) for the R Statistical Environment.
<table>
<thead>
<tr>
<th>Manta ID</th>
<th>Tag Number</th>
<th>Disc Width (cm)</th>
<th>Tag Date</th>
<th>Tag Latitude (°N)</th>
<th>Tag Longitude (°E)</th>
<th>Detection Duration (days)</th>
<th>Total No. Detections</th>
<th>Max No. Consecutive Detections</th>
<th>Max Consecutive Time (hrs)</th>
<th>Deploy Days w/ Multiple Receiver Use (%)</th>
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<td>40.2118</td>
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<td>4449</td>
<td>75</td>
<td>9.97</td>
<td>83.97</td>
</tr>
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</table>

Table 1.2. Tagging summary for nine reef manta rays (*Manta alfredi*) from the Saudi Arabian Red Sea tagged with V16-6H acoustic tags. Columns on consecutive detections refer to detections on a single receiver. The final column refers to days of the deployment for which the individual was detected on multiple receivers within a given day.
Secondary bathymetric correction was applied using an individual’s maximum daily depth and the analyzePsat library in R (Galuardi et al. 2010). In addition to light geolocation, MK10-AF tags acquire and archive locations from the global positioning system (GPS) while the tag is at the surface. In comparison to SPOT tag technology (also manufactured by Wildlife Computers), the MK10-AF tags acquire a more accurate location (SPOTs use the Argos satellite network for positioning while MK10-AF tags use GPS), and MK10-AF tags acquire the location information much more quickly (requiring ~ 0.2 seconds to record a “snapshot” of the GPS constellation).

**Figure 1.2.** Seventy VR2W acoustic receivers deployed in the Al Lith region between 2011-2013 and proportion of combined acoustic detections of *Manta alfredi* tagged with V16 acoustic tags.
1.3.3 Acoustic Telemetry

For improved spatial resolution, nine individuals were tagged with V16-6H acoustic transmitters housed in shark casings (VEMCO, Nova Scotia, Canada) (Table 1.2) using the same attachment methods as above. These coded acoustic tags (Amirix Systems Inc., Nova Scotia, Canada) were set to transmit a unique acoustic signal every 120±30 seconds. The manufacturer estimated a battery life of 1338 days based on transmission delay, power output, and battery type. Seventy VR2W acoustic receivers (37 nearshore, 33 offshore) were deployed in the region between April 2011 and February 2013 to capture transmissions from these tags (Fig. 1.2). Receivers were fixed between 5 - 15 m depth with one of three methods: 1) cement-filled tire for soft sediment 2) bundle of cinder blocks for complex reef topography 3) 3 m long reinforcing bar for reef walls. Two main arrays comprised the majority of receiver effort including one offshore atoll receiver network and one coastal array (Fig. 1.2). Average detection range was 120 m and 530 m at the offshore and inshore array, respectively (Cagua et al. in review). Data was downloaded from the acoustic receivers periodically throughout the study.

1.4 RESULTS

Seven of the nine PSAT tags reported data through the Argos server, and three tags were physically recovered after popup (Table 1.1). Satellite tag deployment durations ranged from 102 - 188 days, and straight-line distances from tag to popup location covered 4 - 169 km (Table 1.1). Based on light geolocation (mP tags), most probable tracks indicated movements were restricted to the greater Al Lith region up to 200 km from the port (Fig. 1.1).
Tags MA111 and MA112 (MK10-AF) reported GPS locations for 60.8% and 29.4% of deployment days, respectively. Little error (± < 100 m) (Moen et al. 1997) is associated with these locations and thus demonstrates an accurate path of travel for these individuals. These tracks indicate frequent movement south of Al Lith within 100 km of the port. Habitat use was largely reef-oriented and coastal, but movement into the nearshore pelagic environment was common, especially in May (Fig. 1.3).

All PSAT tags concurrently recorded depth and temperature measurements along with light levels used for geolocation. The recovered tags yielded an immense dataset (see Chapter 2) that contained a total of > 2.6 million depth records representing a total of

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**Figure 1.3.** Tracks for *Manta alfredi* A) MA111 and B) MA112 tagged with global positioning system (GPS) tags in 2011 demonstrating regional movements, reef affinity, and periodic pelagic excursions.
359 days at liberty. Collectively, mantas spent 19% of time in the surface layer (<2 m) and 84% in the upper 50 m (Fig. 1.4). Yet, four of seven mantas made at least one excursion below 300 m, with one animal reaching a maximum depth of 432 m.

Acoustic deployments ranged from 1 - 342 days. ‘Hotspots’ of activity, as determined by frequent detections of tagged rays, were in coastal waters north and south of Al Lith, while the offshore array never detected tagged rays (Fig. 1.2). Detects occurred throughout the year (Fig. 1.5), and the hour of tag detection was roughly equal throughout a diel cycle. Most individuals also exhibited no apparent seasonality; however, the possibility of seasonal behavior cannot be ruled out for MA107, MA108, MA114, and MA201 (Fig. 1.5). It is likely these fish moved into nearby habitats like those utilized by the GPS-tagged individuals where they would quickly be beyond detection range of our receivers. Acoustic detections also indicated infrequent, short periods of use within range of a single receiver (up to 78 consecutive detections lasting 8 hours) (Table 1.2). In contrast, two or more receivers detected an individual for 43-84% of deployment days (with detections)

Figure 1.4. Composite time-at-depth histogram for all seven reef manta rays with satellite tags. Note changing depth intervals on y-axis and high occupation of surface layer.
demonstrating all individuals frequently travelled among receiver locations and reefs and were detected by up to eight different receivers per day (Table 1.2).

1.5 DISCUSSION

Our satellite and acoustic tagging demonstrate that mantas have an affinity for shallow coastal reef habitats, make occasional use of nearshore pelagic environments, and exhibit site residency, supporting conclusions based on acoustic tagging and photo identification studies in other locations (Indonesia, (Dewar et al. 2008); Hawaii, (Deakos et al. 2011); eastern Australia, (Couturier et al. 2011); Mozambique, (Marshall et al. 2011b). Clark (2010) combined sightings data with active and passive acoustic techniques and discerned high fidelity in all approaches, including multiple observations of 76% (80/105) of photo-identified individuals over the course of a 16-year study. Also, actively tracked individuals inhabited a core area within 6 km of shore while passive monitoring confirmed there was no exchange across a 47 km channel between two arrays. Couturier et al. (2011) also indicated reasonably high re-sighting (48%) on the Great Barrier Reef.

Figure 1.5. Acoustic detections of individual *Manta alfredi* on an array of 70 acoustic receivers deployed near Al Lith, KSA in April 2011 (MA107-114) and April 2012 (MA201-203).
(GBR) but did document a small number of individuals at distant study sites up to 500 km away. Our data yield no indication of this type of behavior in the eastern Red Sea.

Effective design and implementation of conservation measures for vulnerable species relies on robust knowledge of their spatial ecology (Grüss et al. 2011). Recent improvements in telemetry techniques have facilitated the identification of essential or frequented habitats that can be targeted with focused management (Sims 2010). Quantified movements must represent the most holistic estimation of habitat use to maximize effectiveness of derived policy (Couturier et al. 2012) like marine protected area designation (MPAs) (Greene et al. 2009), yet all telemetry technologies have inherent limitations. Thus, an approach employing multiple techniques is necessary to discern a comprehensive understanding of species’ ecology.

PSAT tags without GPS capability proved difficult to geolocate as no individuals undertook movements on a large enough scale relative to inherent error in light geolocation (±0.5° and ±3° for longitude and latitude, respectively) (Lam et al. 2008). Nonetheless, these estimated tracks indicate movements are restricted to the northern Farasan Bank within 200 km of Al Lith and suggest residency to the region for the 6-month period of tag deployment (Fig. 1.1). GPS locations demonstrated significant improvement over light-based geolocation, yielded extremely accurate tracks while individuals were at the surface, and provide further support for regional movements and residency (Fig. 1.3). The acoustic receivers installed on mid-shelf reefs received a small proportion of overall detections (Fig. 1.2) and also demonstrate light use of pelagic areas adjacent to the coast. Repeat detection of several acoustically tagged individuals further corroborates residency (Fig. 1.5). Some individuals disappeared shortly after tagging, but
it is impossible to determine whether this occurred as a product of tag failure or manta departure from the region.

‘Hotspots’ of manta activity, indicated in this study by passive acoustics, were focused along much of the coastal array including around the mouth of Al Lith Harbor and nearshore reefs to the NW and SE (Fig. 1.2). Within these hotspots, mantas exhibited infrequent, short periods of residency on an individual reef; however, movement among reefs was much more common and was focused within the network of shallow reefs near the harbor. Seven of the nine individuals exhibited detection on multiple receivers for at least half of their deployment days, indicating little time was spent occupying a single detection range on a reef when compared to time spent moving among detection ranges of up to eight different receivers per day. Coincidentally, all boat traffic in the area is hosted by the single harbor in Al Lith, and all vessels must cross the coastal fringing reef protecting the harbor via one of two channels in which mantas are commonly observed (pers. obs.). When vessels depart, all of them traverse these channels through the coastal reefs to fish among the nearshore reef network, or the boats navigate through these reefs en route to other fishing destinations further offshore. The ‘hotspots’ of manta activity indicated by the acoustic array occur in areas of high human use and, when combined with a large portion of surface layer occupation and frequent movement among reefs, create the potential for mantas to interact strongly with people.

Vessel strike causes injury and mortality in many marine taxa, including cetaceans (Laist et al. 2001; Van Der Hoop et al. 2013), turtles (Lutcavage et al. 1997; Hazel and Gyuris 2006), and sea cows (Aipanjiguly et al. 2003; Laist and Shaw 2006). For example, collisions have severely affected the endangered North Atlantic right whale
Eubalaena glacialis (Van Der Hoop et al. 2013) and account for 25% of documented Florida manatee Trichechus manatus latirostris deaths (Haubold et al. 2006). Manta rays exhibit similar behavioral characteristics to many of these species, that is, significant occupation of the surface-air interface and frequent use of high traffic regions that may coincide with areas of high productivity. In fact, surface transmitting tags were used on the giant manta ray in Mexico to demonstrate the same potential for strong interaction with ship traffic (Graham et al. 2012). Although we are unable to access boat traffic records for the Al Lith region, opportunistic manta sighting data corroborate the occurrence of vessel strike in this population (Fig. 1.6). Other boat strikes to mantas are thus far unreported in the literature but may present a significant threat to this surface-oriented, docile species.

Entanglement in fishing nets, lines, and anchor rope has also been well documented in many marine groups (Lewison et al. 2004) and represents further consequence for manta-human interaction (Deakos et al. 2011). Individuals in this study demonstrated occupation of the on-shelf reef habitats and almost constant use of the targeted depth range for most fishing activity in the region. Accordingly, mantas near Al Lith are occasionally observed caught in lines and commonly exhibit scarring and open wounds, presumably an artifact of past or recent entanglement. Preliminary sightings results in this study (Fig. 1.6) suggest scarring is in similar proportion to a resident Hawaiian population where 1 in 10 M. alfredi individuals exhibited an amputated or disfigured, non-functioning cephalic fin, and 3% showed clear signs of entanglement in fishing line (Deakos et al. 2011). Although difficult to observe and thus quantify, some
published (Bigelow and Schroeder 1953) and anecdotal (Deakos et al. 2011) evidence demonstrates entanglement in mooring lines often results in manta fatality.

As global elasmobranch populations continue to decline and more no-take zones become designated and enforced, ecotourism operations have developed as an appealing and potentially sustainable alternative to extractive practices (Homma et al. 1999; Deakos et al. 2011; Gallagher and Hammerschlag 2011; Couturier et al. 2012). The aggregative behavior of mantas in many places (e.g. Maldives, Australia, Hawaii, Indonesia, Mozambique) and their approachability by divers and snorkelers has made this charismatic species popular with tourists (Couturier et al. 2012). In many of these areas, substantial ecotourism operations have developed resulting in economic benefits reaching into the millions (USD) (Homma et al. 1999; Anderson et al. 2011b; Gallagher and Hammerschlag 2011). Although a non-extractive process, poorly managed tourist operations can elicit lethal and serious sub-lethal impacts on targeted manta populations as a consequence of high pressure from divers, snorkelers, and increased boat traffic. This may already be occurring at many aggregation sites. For example, mantas appear to have

Figure 1.6. (A) Prop scarring and (A,B) line entanglement found on two *Manta alfredi* during spring 2013. Note line on pectoral margin and large line gash on (A) manta’s right-upper cephalic fin. (A) cephalic fin also exhibits significant damage.
abandoned a previously frequented area in Bora Bora (De Rosemont 2008) following a rapid increase in tourism at the aggregation. Thus, great care must be taken to develop ecotourism policies and practices; corresponding enforcement and monitoring must also be established.

Fisheries are the most direct threat to many elasmobranch species and have recently garnered heavy scrutiny for the predicted and realized effects on target populations (Dulvy et al. 2008; Ferretti et al. 2010). Harvest of elasmobranchs is illegal in Saudi Arabia, yet we have observed sharks and rays on numerous fishing vessels and these animals regularly number in the hundreds at the local market. However, despite these observations, it is unlikely that significant fishing pressure is currently exerted specifically on mantas in the Saudi Arabian Red Sea. An extensive survey (every two weeks for two years) in one of the Red Sea’s largest fish markets (Jeddah, KSA) yielded no manta observations and only five Mobula sp. (J. Spaet, pers. comm.) In addition, fishermen interviews suggest no directed harvest for mantas is currently underway by local fishermen in this region (J. Spaet, pers. comm.). However, this does not negate the possibilities of foreign-based vessels, international landings, and significant bycatch components. Although data is lacking, manta susceptibility to harvest is considered high and should fishing or significant by-catch occur in this area, local populations will suffer. Regional declines are unlikely to be alleviated by immigration or reproduction due to the life history of mantas, including infrequent reproduction, small litters, and limited large-range movement (Couturier et al. 2012).

An accurate depiction of animal behavior is paramount for the design and implementation of appropriate management techniques. The combination of multiple
telemetry approaches employed here capitalizes on the strengths of different techniques and aids in alleviating some of the limitations. This approach is so far unique to this species and the Red Sea region and is critical for identifying potentially hazardous human-manta interaction. The susceptibility of batoids is cause for serious concern. Future work should seek a robust method to quantify realized anthropogenic effects on manta populations.
Chapter 2: Detailed Diving Behaviors of the Reef Manta Ray (*Manta alfredi*) in the Saudi Arabian Red Sea

2.1 ABSTRACT

Recent efforts have significantly improved information available for many devil ray populations worldwide, including seasonal migration, oceanographic influences, mating, and others. Yet, Red Sea manta rays remain completely enigmatic. We deployed pop-up satellite archival tags on nine reef manta rays, *Manta alfredi*, to elucidate diving behaviors and vertical habitat use that could better inform our understanding of manta ecology. Adequate data was obtained from seven tagged mantas. This included three recovered tags containing full archival datasets recording depth, light, and temperature every 10-15 seconds that resulted in over 2.6 million datapoints for three individuals. Mantas frequented the upper 10 m during daylight hours and tended to occupy deeper water throughout nocturnal periods. Six of the seven individuals performed a cumulative 76 deep dives (>150m) with one individual reaching 432 m, extending the known depth range of this coastal, reef-oriented species and confirming its role as an ecological link between epipelagic and mesopelagic habitats. High-resolution dive data for 3 individuals represented 62 dives over 150 m. An investigation of mean vertical velocities during deep dives suggested that mantas may utilize gliding behavior during travel and that this behavior may provide significant efficiency benefits over continuous horizontal swimming. This study is the first to use satellite telemetry to investigate vertical behaviors and habitat use of the reef manta and is the first in-depth dive analysis focused on mantas of the Red Sea.
2.2 INTRODUCTION

The reef manta ray (*Manta alfredi*) is a small, coastal mobulid (Family: *Mobulidae*) that exhibits typical K-selected life history traits including slow maturation rate; small, infrequent litters; and long lifespan (Couturier et al. 2012). Sighting records suggest preferential occupation of nearshore tropical waters with strong site affinity and limited movements (Marshall et al. 2009) although horizontal excursions >500 km have been documented (Couturier et al. 2011). Movements of *M. alfredi* coincide with predictable manta aggregations at several known locations in tropical and subtropical waters (Couturier et al. 2012) associated with mating, cleaning, food availability, and currents (Dewar et al. 2008; Anderson et al. 2011a; Couturier et al. 2011; Jaine et al. 2012).

Few aspects of manta biology and ecology have been adequately described, yet recent efforts have dramatically increased our knowledge about this enigmatic group (Couturier et al. 2012). Some information is now available about horizontal movements of reef manta rays (Dewar et al. 2008; Clark 2010; Couturier et al. 2011; Deakos et al. 2011), but vertical habitat use remains largely undescribed. An understanding of vertical movements is crucial for understanding a species’ ecology, including site occupation, feeding/mating behavior, habitat use, and potential anthropogenic interactions. *Manta alfredi* was recently designated “Vulnerable to Extinction” by the IUCN and is listed on Appendix II of the Convention on International Trade in Endangered Species and Appendices I and II of the Convention on Migratory Species. Thus, ecological information is of paramount importance for developing adequate management and conservation strategies.
Satellite telemetry has been employed to elucidate the ecology of a diverse group of marine vertebrates (Skomal et al. 2009; Block et al. 2011; Womble and Gende 2013). These insights have provided an ecological framework around which management efforts can be constructed. Recent advances in satellite telemetry technology have enabled longer term tracking over significantly larger spatial scales than previous techniques. Pop-up satellite archival (PSAT) tags are a recent development that facilitates in-depth investigation of animal ecology by archiving high-resolution records of an individual’s diving behavior (Thorrold et al. in review). Until now, investigation of vertical movements in *M. alfredi* has been limited to active acoustic tracking that provides high-resolution depth data over short timescales (up to 103 hours continuously) (Clark 2010; Deakos et al. 2011; Papastamatiou et al. 2012).

This study is the first to utilize satellite telemetry techniques to elucidate vertical behavior of *Manta alfredi*. Here, we seek to characterize temporal trends, habitat use, and deep diving in relation to manta ecology.

### 2.3 METHODS

Nine *M. alfredi* were tagged with pop-up satellite archival tags (PSAT) in the south-central Red Sea (Fig. 2.1) during spring 2011 and 2012 (5 miniPAT, 4 MK10-AF; Wildlife Computers Inc., USA) (Table 1.1). Tags were attached to a stainless steel dart with small diameter cable and applied by a freediver into the dorsal musculature near the midline with a sling spear.

Tags archived light level, depth, and water temperature every 10 and 15 seconds for the MK10-AF (MK10) and miniPAT (mP), respectively. Data was processed onboard
the tag to summarize the desired information for transmission via the Argos satellite system. Proportion of time spent in various vertical habitats was described daily by 14 (mP) or 16 (MK10) temperature and depth bins. Depth-temperature profiles were assembled internally over 24 (mP) or 12 (MK10) hour periods. High-resolution (mP: 450 sec, MK10: 75 sec) depth data was recorded constantly (mP) or cycled one week on with two weeks off (MK10) for the duration of tag deployment. At pre-programmed deployment durations of 100 (MK10) or 180 (mP) days, tags automatically popped off the animal using a corrosive burn wire. After the tags released and floated to the surface, the tags attempted to transmit packets of summarized data via Argos satellites until battery failure.

Transmitted and archival data was decoded with manufacturer software, and all subsequent analyses were conducted in the R Statistical Environment (R Core Team

Figure 2.1. (A) Location and (B) study site maps with tagging locations of nine satellite tagged *Manta alfredi* near Al Lith in the eastern Red Sea.
using packages ‘stats’. Values are expressed as mean ± SD unless stated otherwise. Dive data was delimited into day (6am-6pm) and night (6pm-6am), and a Two-sample Kolmogorov-Smirnov (K-S) test was performed to compare diel changes in depth distributions. A Student’s t-test was used to compare mean day and nighttime depths. Linear least-squares regression was used to assess correlations between mean nightly depth and moon phase for each individual and a pooled dataset of all individuals. Lunar illumination data were obtained from the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.php, accessed Apr 2013) and arcsine-transformed before statistical analysis (Zar 1996).

Further analysis of archival data included investigation of overall dive velocities, total vertical distance travelled, and rhythmic and deep diving behaviors. Velocity histograms (m.s\(^{-1}\)) were calculated for archival datasets (tags MA001, MA006, and MA007) as depth change over the 10 (MK10) or 15 (mP) second interval recorded by the PSAT tag. Total vertical distance traveled for each diel cycle was computed as grand sum of depth change per day and night period. Dive series was examined for rhythmic elements using autocorrelation functions in R. Finally, deep dives were defined as maximum depth > 150 m with dive start/stop depths < 15 m.

**2.4 RESULTS**

Tag deployments lasted between 102 - 188 days. Four PSATs transmitted summarized data representing 5.3 - 54.7% of days over deployment duration. Two MK10-AF tags did not report, and three tags were physically retrieved. Recovered tags yielded full depth,
temperature, and light level records every 10 (MK10) or 15 (mP) seconds for the duration of deployment (Table 1.1) and cumulatively recorded >2.6 million time-stamped records.

Overall daily vertical habitat use indicates nearly constant occupation of the upper 50 m of the water column (Figs. 2.2-4) with sporadic use of deeper water down to 432 m (Fig. 2.2c), extending the current depth range for *M. alfredi* by over 100 m (Marshall et al. 2011a). Mantas also exhibited distinctly different diel vertical behavior (Fig. 2.4). True depth distribution during daytime was skewed toward the upper layers and differed significantly from the nocturnal occupation of deeper waters (K-S Test p = 0.000). In addition, mean daytime depth for each individual (Table 2.1) and all individuals (21.7 ± 23.4 m) was significantly shallower than nighttime (34.2 ± 21.0 m; t-test p = 0.000).

Finally, regression analyses indicated that mean nightly depth was unrelated to lunar illumination for 6 of 7 individuals (Table 2.1, Fig. S1) and for the aggregate nightly depth data (R² = 0.000, Fig. S1). Only one individual exhibited a slope of the regression line significantly different from 0 (MA007, p < 0.03) and demonstrated poor variance explanation by the regression model (R² = 0.047, Fig. S1).

Three recovered tags facilitated further analysis of high-resolution datasets. Vertical behaviors were dominated by slow ascents/descents (< 0.25 m.s⁻¹) although maximum rates of 2.27 and 1.87 m.s⁻¹ were recorded for descent and ascent, respectively (Fig. 2.5). Despite slow depth changes, these fish exhibited highly variable cumulative daily vertical movements that ranged 2870 - 10300 m. One of three archival datasets showed only marginally more vertical movement during day (mean total daytime movement 2804 ± 725 m and night 2528 ± 589 m, p = 0.003) while the other two
Figure 2.2. Daily ambient water temperature (indicated by color) and depth (y-axis) experienced by *Manta alfredi* for the duration of satellite tag deployment in 2011 near Al Lith, Kingdom of Saudi Arabia. (A) Manta identification number MA106 (B) MA102 (C) MA105 (D) MA104 (E) MA112 (F) MA111. Black points at the bottom of panels (E) and (F) indicate days for which the satellite tags resolved FastLoc GPS locations.
Figure 2.3: Daily time-at-depth (%) indicated by the color across the y-axis by *Monachus* spp. for the duration of satellite tag deployment in 2011 near Al Lith, KSA. (A) Manta identification number MA106, (B) MA102, (C) MA105, (D) MA104, (E) MA112, (F) MA111. Black points at the bottom of panels (E) and (F) indicate days for which the satellite tag was not resolved. GPS locations.
exhibited no difference over the diel cycle. In addition, no rhythmic components were found using autocorrelation analyses. All tag data recorded 76 partial deep dive profiles while the archival depth record captured 62 complete deep dives over 150 m that were distributed randomly throughout a daily cycle. The majority of descent rates for the cumulative deep dive record (with no depth change values removed) were between 0 - 0.10 m.s\(^{-1}\) while ascent rate frequency distribution was skewed toward slightly faster depth changes (Fig. 2.6).

<table>
<thead>
<tr>
<th>Manta ID</th>
<th>Day Depth (m)</th>
<th>Night Depth (m)</th>
<th>Max Velocity (m.s(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean±SE</td>
<td>Max</td>
<td>Mean±SE</td>
</tr>
<tr>
<td>MA102</td>
<td>24.3 ± 0.48</td>
<td>341</td>
<td>36.0 ± 0.37</td>
</tr>
<tr>
<td>MA103</td>
<td>23.7 ± 0.65</td>
<td>59</td>
<td>35.0 ± 0.61</td>
</tr>
<tr>
<td>MA104</td>
<td>23.1 ± 0.50</td>
<td>363</td>
<td>33.9 ± 0.37</td>
</tr>
<tr>
<td>MA105</td>
<td>35.1 ± 0.36</td>
<td>312</td>
<td>47.6 ± 0.30</td>
</tr>
<tr>
<td>MA106</td>
<td>21.2 ± 0.04</td>
<td>392</td>
<td>35.3 ± 0.03</td>
</tr>
<tr>
<td>MA111</td>
<td>20.0 ± 0.03</td>
<td>214</td>
<td>32.7 ± 0.03</td>
</tr>
<tr>
<td>MA112</td>
<td>23.5 ± 0.04</td>
<td>362</td>
<td>34.7 ± 0.03</td>
</tr>
</tbody>
</table>

Table 2.1. Statistical results for vertical habitat use and diving behaviors of seven reef manta rays in the Saudi Arabian Red Sea tagged with pop-up satellite archival tags (PSAT). * indicates daytime depth distribution strongly skewed toward upper layers compared to nocturnal depth occupation (p=0.000). \(\ast\) indicates p<0.05.

Figure 2.4. Distribution of percent time-at-depth (m) during day (grey) and night (black) from aggregate depth records for nine *Manta alfredi* in the eastern Red Sea.
Isolation of a single series of consecutive dives further highlights characteristic deep-diving behavior (Fig. 2.7).

![Archival vertical velocity (m.s\(^{-1}\)) from three archival satellite tag datasets collected every five (miniPAT) or ten (MK10-AF) seconds for the duration of tag deployment on Manta alfredi. Zero velocities (no depth change) were dropped from plotting to facilitate visualization of non-zero values. Grey and black bars indicate day and night, respectively.]

**Figure 2.5.** Archival vertical velocity (m.s\(^{-1}\)) from three archival satellite tag datasets collected every five (miniPAT) or ten (MK10-AF) seconds for the duration of tag deployment on *Manta alfredi*. Zero velocities (no depth change) were dropped from plotting to facilitate visualization of non-zero values. Grey and black bars indicate day and night, respectively.

### 2.5 DISCUSSION

Similar to the few mobulids with quantified vertical habitats (Rubin et al. 2008; Clark 2010; Canese et al. 2011), mantas exhibited frequent use of the upper epipelagic layer (< 60 m) throughout a diel cycle. Daytime vertical habitat use was indicative of surface occupation, and we observed these rays frequently feeding in the top 10 m; during the nocturnal period, mantas inhabited deeper water. Several active and passive acoustic studies have suggested movement away from reef environments and into deeper water at night. Upwelling events in the Maldives led Anderson et al. (2011a) to speculate, based on field observations, that mantas regularly utilize a deep zooplankton layer at night when these prey items perform diel vertical
migration (DVM), and only during major upwelling events does this layer reach the surface where large groups of mantas are observed feeding. Similarly, manta detections on passive acoustic arrays have been shown to drastically decrease during nocturnal periods leading these authors to draw similar nighttime feeding conclusions (Dewar et al. 2008). In addition, Clark (2010) found all actively tracked mantas made similar offshore excursions during night and utilized deeper water. Until now, however, this behavior was observed in a few actively tracked animals over a relatively short duration (up to 150 hours) (Clark 2010) or speculated based on passive acoustics (Dewar et al. 2008; Deakos et al. 2011). This study quantifies diel depth changes integrated over several months. Thus, we conclude the frequency of this behavior is high and doesn’t fluctuate seasonally suggesting it is a dominant behavior in manta ecology.

Nocturnal occupation of deeper water has been suggested as a means to increase foraging opportunities in other marine species, including filter feeding elasmobranchs (Nelson et al. 1997; Graham et al. 2006; Shepard et al. 2006; Sims et al. 2006) and may be a strategy for mantas to exploit the rising layer of mesopelagic zooplankton that move into the photic zone at night (Gliwicz 1986; Yahel et al. 2005) or the demersal plankton emerging from the reef benthos (Yahel et al. 2005). In the Red Sea, it is clear that significant plankton biomass moves shallower at night both from deeper layers in the pelagic environment and the benthos in reef environments and could provide a valuable food source to a largely epipelagic species in an otherwise very oligotrophic environment (Yahel et al. 2005; Klevjer et al. 2012).

Although light has been indicated as a major factor driving vertical behavior of many large pelagic fish like billfishes (Carey and Robison 1981; Abascal et al. 2010) and
sharks (Musyl et al. 2011), the direct effects of light, and specifically lunar illumination, on mobulids is unclear. To date, only passive acoustic studies have been able to make inferences about the effects of lunar cycle on manta behavior (Dewar et al. 2008; Clark 2010; Jaine et al. 2012). This study is the first to perform regression analysis to elucidate the effects of lunar illumination on nocturnal habitat use of mantas. It is clear that mantas in this study didn’t alter vertical utilization with progression of moon phases, which may be a product of regional oceanography. Currents in the Red Sea are predominately driven by winds (Patzert 1974) rendering tidal and lunar cycles relatively unimportant in water movements. In

Figure 2.6. Frequency histogram for 62 deep dives over 150 m conducted by three individual reef manta rays. Zero velocities (no depth change) were dropped from plotting to facilitate visualization of non-zero values. Grey and black bars indicate day and night, respectively.
contrast, areas like northern Indonesia and the Great Barrier Reef exhibit tidal-driven (and thus also lunar) oceanographic patterns that likely provide feeding opportunities for planktivorous fish (Dewar et al. 2008; Jaine et al. 2012). In addition, nighttime depth of mantas exploiting reef-derived plankton as a nocturnal food source would likely be unaffected by lunar illumination.

Mantas demonstrated utilization of the full temperature range in the epi- and mesopelagic layers of the Red Sea (range 21.6-34.2°C) with dives > 400 m. This behavior represents a significant ecological coupling of shallow and deep reef habitats. Deep dives occurred relatively infrequently throughout all but one deployment and were characterized by asymmetrical V-shaped dive profiles with extremely short bottom times, relatively slow descents, and faster ascents. Although these dives may be feeding-oriented to exploit the relatively rich zooplankton layers below 200 m in the Red Sea (Klevjer et al. 2012), this motivation seems unlikely. Mantas in this area are regularly observed surface feeding throughout daylight hours and presumably move slightly deeper (mean all individuals: 36.5 m) at night for nocturnal feeding. Thus, it is improbable that resource availability would encourage mantas to feed down to > 400 m. Searching is also a questionable motivation for this behavior as this would suggest occasional discovery presumably indicated by dive termination and occupation of that layer. None of this behavior was observed in any of the 76 deep dives performed by 6 individuals in this study. Finally, these dives may be a byproduct of travelling behavior in which mantas perform gliding dives to conserve energy and maximize movement efficiency. Although our tags didn’t record pitch angle and tail-beat frequency data, vertical descent velocities for the three high-resolution datasets were heavily skewed toward slower depth change
than ascents (Fig. 2.6). Accurate tag locations were relatively infrequent and do not permit calculation of horizontal distance travelled for any given deep dive or bout of dives. However, geolocations do suggest on several occasions that deep diving bouts occurred between two known locations up to 65 km apart over a three-day period. The flattened descent profile of a single series of consecutive deep dives that results from this behavior provides further visual support for the glide hypothesis and demonstrates what appears to be a largely passive descent followed by active ascent (Fig. 2.7). These descent rates are similar to those recorded for Japanese flounder (Takagi et al. 2010). In addition, manta ascent and descent vertical velocities exhibit the same relationship as lateral acceleration during ascent and descent in whale sharks, that is, very slow descent

![Graphs showing depth and vertical dive velocity over time](image)

**Figure 2.7.** (A) Consecutive deep diving behavior exhibited by MA006 initiated at 0900 on 22 May 2001 and (B) the corresponding mean vertical velocity histogram. Negative velocities describe descents. Red segments indicate descent velocity between depth points < 0.1 m.s\(^{-1}\) which we suggest corresponds to gliding behavior.
while consistently reaching 0.10 m.s\(^{-1}\) upon ascent (Gleiss et al. 2011).

Gliding in fishes involves harvesting kinetic energy from potential that is derived from the fish’s negative buoyancy upon descent. This is a very efficient strategy for movement in an aqueous medium and may decrease drag threefold compared to active swimming (Weihs 1973). Exceptional glide performance has been demonstrated in both Japanese flounder (*Paralichthys olivaceus*) (Takagi et al. 2010) and whale sharks (*Rhincodon typus*) (Gleiss et al. 2011). *R. typus* has large, flat pectoral fins that aid in passive descent while *P. olivaceus* exhibits significant dorso-ventral flattening capable of producing substantial lift. Mobulid rays also boast an extreme amount of flattening facilitated by enormous pectoral fins that behave like bird’s wings underwater and may possess among the most well suited body types for maximizing glide efficiency. Morphological traits for efficient movement (i.e. dorso-ventral flattening and wing-like pectoral fins) combined with negative buoyancy make powerless glide diving followed by active ascent a more energetically efficient strategy for traversing horizontally than continuous swimming (Takagi et al. 2010) and may provide significant energetic benefits to mantas during travel.

An understanding of vertical movements is necessary to characterize habitat use and ecology of poorly understood marine species. Until now, manta vertical behaviors have remained largely enigmatic rendering the management and conservation of this vulnerable species increasingly difficult. Future work should apply the ever-increasing body of new tagging technologies to mobulids in order to illuminate diving behaviors in three dimensions (Yoda et al. 2001; Semmens et al. 2013), sample the experienced prey
CONCLUSION

This thesis demonstrates the utility of a multifaceted approach to understanding a species’ ecology and the value of acquiring data at varying resolution across multiple spatial and temporal scales. These mantas utilize a large portion of the region’s coastal area in addition to occasionally occupying the nearshore pelagic environment. Clear ‘hotspots’ of activity were evident from the acoustic tagging, demonstrating significant overlap with areas of high human use and further exacerbating the issue of anthropogenic effects on vulnerable manta populations. Opportunistic sighting data strengthens the supposition of serious human impact on this population.

The investigation of vertical behaviors validated previous hypotheses of nocturnal reef departure and frequent use of the surface layer during the day. It also extends the known depth range of *Manta alfredi* to 432 m and suggests gliding behavior may be a significant component of manta diving, which could provide considerable increases in movement efficiency. The exact reason for this type of movement (feeding, traveling, resting, etc.) is not clear and deserves further study.

Future work should seek to accurately identify and quantify realized anthropogenic effects on this population. In addition, new tagging technologies are rapidly evolving and may provide the opportunity to deepen our understanding of manta behavior in this poorly studied region.
Figure S1. Moon fraction regression with mean daily nighttime depth for individual reef mantas (A) MA106 (B) MA102 (C) MA103 (D) MA105 (E) MA104 (F) MA112 (G) MA111 and (H) all mantas tagged with satellite tags in the Saudi Arabian Red Sea.
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